

Invertebrates in Canopy and Ground Organic Matter in a Neotropical Montane Forest, Costa Rica¹

Nalini M. Nadkarni² and John T. Longino³

Department of Biological Sciences, University of California, Santa Barbara, California 93106, U.S.A.

ABSTRACT

In a neotropical cloud forest of Costa Rica, we compared the density and composition of macro- and mesoinvertebrates in organic matter found within the canopy to that found in the upper soil horizons on the forest floor. We used a Winkler sifting apparatus to extract invertebrates from accumulated litter and humus. The numerically dominant invertebrate groups in both canopy humus and forest floor leaf litter were mites, adult beetles, holometabolous insect larvae, ants, collembola, amphipods, and isopods. Relative abundances of these major taxa were the same in canopy and on the forest floor, indicating that canopy organic matter shares a fundamentally similar invertebrate community with forest floor. All of these groups except ants had significantly higher densities in the canopy, with a mean density 2.6 times greater on the ground than in the canopy. Ant density was similar in both microhabitats.

A MAJOR PORTION OF FOREST NUTRIENT CYCLING research has focused on the storage and circulation of dead organic matter because it is important as an energy source for heterotrophs and as a reservoir for plant mineral nutrients (Brown & Lugo 1982, Dickenson & Pugh 1974, Swift *et al.* 1979). Because litterfall is a major pathway of nutrient and energy flux in most forests, almost all of this research has focused on the abscised plant material located on the forest floor (Bray & Gorham 1964, Proctor 1983, Vitousek & Sanford 1986). In addition to litter on the forest floor, however, many tropical and some temperate wet forests support a substantial pool of organic matter that resides on tree branches and trunks. The standing crop of live and dead organic matter in forest canopies ranges from 1.4 to 14.0 t/ha, and reaches a maximum in montane tropical cloud forests (Golley *et al.* 1971; Pócs 1980; Nadkarni 1984, 1985). Epiphytes, parasitic plants, vines and their associated fauna make up the live portion. The dead component, termed "crown humus" by Jenik (1973), is derived from intercepted nutrients in rain, mist, and dust, litter intercepted from overstory trees, abscised epiphyte tissues, decomposing bark, and the detritus of canopy dwelling animals. Dead organic matter in the canopy comprised approximately half of the total canopy organic matter in a tropical cloud forest

where live and dead canopy components were estimated separately (Nadkarni 1984).

One important functional aspect of dead organic matter is the composition and abundance of the detritivore fauna it supports. In addition to the pools of nutrients and energy in their own biomass, detritivores participate in the regulation of nutrient transfer. Invertebrates are the main agents of litter fragmentation and mixing of leaf litter with mineral soil, exposing a greater surface area for microbial colonization (Edwards *et al.* 1970, Crossley 1977, Collins 1980, Seastedt 1984).

Although there are numerous anecdotal accounts, canopy dwelling litter invertebrates in the tropics have never been systematically sampled. These include descriptions of earthworm diversity and distribution (Lyford 1969), accounts of bird foraging in arboreal leaf-litter (Remsen & Parker 1984, Greenberg 1987, Nadkarni & Marelson 1989) and enumerations of invertebrates residing within tank bromeliads and other phytotelmata (*e.g.*, Pittendrigh 1948, Fish 1983). In this paper, we quantitatively compare the composition and abundance of invertebrates that inhabit canopy and ground litter and humus in a neotropical montane forest.

MATERIALS AND METHODS

Field research was conducted in and near the Monteverde Cloud Forest Reserve (MVCFR), in west central Costa Rica (10°18'N, 84°48'W), from 10 June to 30 August 1984. This area encompasses three of the five biotic communities recognized by Lawton and Dryer (1980): Elfin Woodland, Leeward Cove Forest, and Leeward Ridge Forest. Soils

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² Present address: The Marie Selby Botanical Gardens, 811 South Palm Avenue, Sarasota, Florida 34236, U.S.A.

³ Present address: Allyn Museum of Entomology, 3621 Bay Shore Road, Sarasota, Florida 34234, U.S.A.

are moist or wet all year. Well-developed root systems occupy the upper 0–15 cm of soil, and substantial amounts of organic matter are incorporated into the upper horizons. A litter layer of 2–8 cm overlies the upper soil horizon all year (Lawton 1980, Nadkarni & Vance, unpub. data).

Relative to the forest floor, the upper tree canopy experiences more wind (Lawton 1980), more frequent mist, higher air temperature maxima, and more frequent wetting/drying cycles (Nadkarni & Vance, unpub. data). These conditions foster an extremely abundant and diverse epiphyte community with an estimated 4730 kg/ha of canopy organic matter. Unlike many other tropical and temperate forests, there is little apparent difference in the amounts of live and dead organic matter supported by trees of different species; nearly all of the branch interiors, crotches, and trunks of mature trees are covered with thick epiphyte mats (Lawton & Dryer 1980).

Trees from which samples were taken were chosen to include the largest size classes of the most common tree species in this forest (Lawton & Dryer 1980). The eight sample trees included *Clusia alata* (Guttiferae) (1 individual); *Didymopanax pittieri* (Araliaceae) (2); *Quercus* sp. (Fagaceae) (1); *Pouteria viride* (Sapotaceae) (1); and *Ficus* sp. (Moraceae) (3). All trees supported large accumulations of live epiphytes and contiguous mats of crown humus on trunks and interior branches. We climbed trees with the modified mountain climbing techniques of Perry (1978). These single rope techniques restricted the area from which we collected material to the interior branch regions of the mid- and lower crown (7 to 17 m above ground, 0 to 5 m from central trunk), the area where nearly all the dead organic matter within tree crowns is located.

Litter invertebrates were sampled by sifting bulk litter and humus through a 9 mm² mesh sieve, which greatly increased the amount of material and spatial area from which we sampled invertebrates. Approximately 17 liters of this bulk dead organic matter produced 1 liter of sifted litter, and each sample consisted of 2 to 8 liters of sifted litter. Total bulk litter sampled was 884 liters from the canopy and 816 liters from the ground. Bulk dead organic matter in the canopy was collected by sifting available "canopy standing litter" (host tree and epiphyte leaves and leaf parts, reproductive parts, and twigs resting on branches) and crown humus on accessible branch interiors, branch crotches and trunks. For each canopy sample, a paired ground sample was obtained. Litter was selected haphazardly from accumulations on the forest floor below until a volume

of sifted material similar to the canopy sample was obtained. Samples were always taken in pairs (with matched final volumes) so that site and weather specific covariates could be factored out in paired sample statistical analyses.

Invertebrates from sifted litter were extracted using Winkler extractors (Ward 1987), a passive extraction technique in which the sifted litter is suspended over a cup of alcohol and left to air-dry. Invertebrates slowly leave the drying litter and fall into the alcohol. We allowed our samples to air-dry in the MVCFR field laboratory for three days. Invertebrates were sorted with a dissecting microscope and all organisms that were easily visible at 10 \times power (greater than about 0.5 mm in length) were counted. Invertebrates were separated into seven categories: mites, adult Coleoptera, holometabolous insect larvae, adult ants, Collembola, Crustacea (amphipods and isopods), and other. Because the biology of these litter groups is so poorly known, no attempt was made to classify them into ecological categories such as predators, herbivores, etc. Data were tabulated in terms of number of individuals per liter of sifted litter. For each category, ground *vs.* canopy differences in density were tested with a paired *t*-test ($P < 0.05$).

RESULTS AND DISCUSSION

The numerically dominant taxa in both canopy and ground dead organic matter were Acarina (mites), adult Coleoptera (beetles), holometabolous insect larvae, Formicidae (ants), Collembola (springtails), and Crustacea (amphipods and isopods). Members of these taxa are no doubt the major agents of fragmentation of organic matter at our study site, as they are in other tropical montane regions (Collins 1980, Pearson & Derr 1986, Leakey & Proctor 1987). The only striking difference with other studies at similar elevations was the paucity of oligochaetes at our site, both in the canopy and on the forest floor. This contrasts with the invertebrate fauna of a Costa Rican lower montane moist forest (Atkin & Proctor 1988), where earthworms constituted a major part of the density and biomass of the litter fauna. This contrast may be due to differences in sampling techniques, whereby the hand-sorting methods used by Atkin and Proctor underestimated meso- and micro-arthropods, and our sifting techniques underestimated soft-bodied annelids.

Relative proportions of these major taxa were the same in canopy and ground dead organic matter, showing that the canopy shares a fundamentally

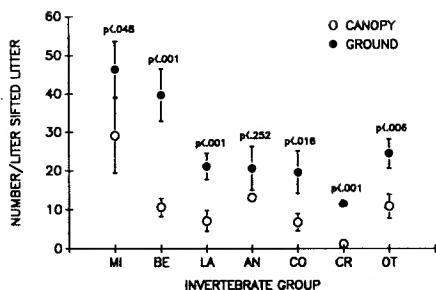


FIGURE 1. Invertebrate density (number of individuals/liter of sifted litter) by invertebrate group for ground and canopy samples. MI = mites, BE = adult beetles, LA = holometabolous insect larvae, AN = adult ants, CO = Collembola, CR = amphipods and isopods, OT = other (Hemiptera, Homoptera, Orthoptera, Dictyoptera, Dermaptera, adult Diptera, Thysanoptera, parasitic Hymenoptera, Apterygota, Symphyla, millipeds, centipeds, spiders, other Arachnida, Gastropoda, Annelida). Significance values above categories are results of paired-sample *t*-tests. Error bars represent two standard errors of the means.

similar invertebrate community with the forest floor (Fig. 1). Total invertebrate abundance was higher on the ground than in the canopy for all 8 sample pairs, with a mean density 2.6 times greater on the ground than in the canopy. Six of the seven invertebrate categories were significantly less abundant in the canopy (Fig. 1). Ants were the exception, exhibiting no consistent differences between canopy and ground. Mite densities were only slightly (but significantly) lower in the canopy. The remaining categories differed strongly between canopy and ground. Dead organic matter in the canopy was clearly depauperate in beetles and larvae. Terrestrial crustaceans, the largest invertebrates in the samples, were readily visible on the ground, but rarely seen in the canopy samples.

What factors might explain lower invertebrate densities in the canopy? Differences in microclimate could affect their composition and abundance. In general, tree crowns are subject to greater amounts of insolation, wind, and more frequent wetting/

drying cycles than the forest floor (Cachan 1963, Hosokawa *et al.* 1964, Lawton 1982, Chazdon & Fetcher 1984). Numerous studies have documented sensitivity of invertebrates to microclimatic regimes, particularly moisture, temperature, and insolation; many important detritivore groups tend to drop out with increasing desiccation. Terrestrial crustaceans, for example, are very sensitive to moisture conditions (Edwards 1974) and were very rare in our canopy samples. Difficulties of dispersal to the canopy and/or within crowns of trees may exist for particular invertebrate groups, especially many of the sedentary groups and those living in nest structures or galleries (Moran & Southwood 1982, Adis *et al.* 1984, Seastedt 1984, Stork 1987). Litter substrate differences may cause differences in invertebrate populations. Little published data exist for differences in canopy and forest floor organic matter, but preliminary data suggest that they differ greatly in a variety of physical and chemical characteristics (Nadkarni & Vance, pers. comm.).

Elucidation of which factors depress invertebrate density in the canopy, and conversely, which canopy organic matter characteristics may be caused by depressed invertebrate density, await further investigation. We have shown that canopy-held organic matter, an ecosystem component of tropical montane forests, differs from forest floor organic matter in an important biotic characteristic. This implies that organic matter in the canopy should be treated as a separate compartment in ecosystem studies, and cannot be subsumed under studies of organic matter on the forest floor.

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